Using functional Magnetic Resonance Imaging repetition suppression to explore the neural representation of natural scenes

Honors Thesis Research

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by

Thomas P. O'Connell

The Ohio State University
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Project Advisors:

Professor Dirk Bernhardt-Walther, Department of Psychology

Professor Per Sederberg, Department of Psychology

Abstract

Natural scene perception is a fundamental cognitive process with great relevance to human cognition and behavior. The human brain and visual system constantly extracts information and context from natural scenes to make predictions about the future and plan behaviors. Previous research has identified the parahippocampal place area (PPA), the retrosplenial cortex (RSC), and the transverse occipital sulcus (TOS) as brain regions responsible for discriminating natural scene categories (Walther et al., 2009; Dilks et al., 2013) and determined that blocks of color photographs (which contain color, texture, and structure) and contour line drawings (which contain just structure) yield equivalent category-specific patterns of activation in PPA and RSC (Walther et al., 2011). Repetition suppression (RS) is the reduction in neural activation magnitude that occurs across multiple presentations of a stimulus (Grill-Spector et al., 2001). RS can be used to determine representational similarity for superficially different stimuli. To date, little research has investigated the role of structural information in the formation of neural representations for individual scenes within a category. We used fMRI to measure RS between pairs of color photographs and line drawings to explore what features are contained in neural representations for individual scenes in PPA, RSC, and TOS. Results indicate that individual color photographs and line drawings depicting the same scenes are representationally dissimilar in PPA, RSC, and TOS. While prior research shows that the structure of a scene is sufficient for PPA and RSC to encode scene category, the current study provides evidence that PPA, RSC, and TOS encode an array of information from individual scenes, including color, texture, and structure. This research expands scientific understanding of the neural processes underlying natural scene perception by highlighting the different information used to represent scene identity versus scene category.

Introduction

Functional Magnetic Resonance Imaging (fMRI) is a state of the art brain imaging technique that has recently revolutionized the field of cognitive neuroscience. In blood-oxygen-level-dependent (BOLD) fMRI, blood flow throughout the brain is measured using magnetic properties of deoxygenated blood. The hemoglobin of deoxygenated blood contains ferrous iron, which causes magnetic disturbances detectable by a magnetic resonance field (Thulborn et al, 1982). When neurons within a brain region are activated by a stimulus, they consume more oxygen than at rest neurons in other regions of the brain. This depletion of oxygen causes an initial influx of deoxygenated blood in an activated region, followed by an increase in levels of oxygenated blood. The influx of deoxygenated blood immediately after neuron activation causes an inhomogeneity in the magnetic resonance field that is gradually diminished by the replenishment of oxygenated blood (Turner et al, 1991). The washing out of these magnetic inhomogeneities by the return of oxygenated blood is called the hemodynamic response function (HRF) and is the main effect measured by BOLD fMRI techniques.

In the past fifteen years, researchers have used fMRI to identify which brain regions facilitate perception of natural scenes. Natural scenes are complex environments that exist in the world, as opposed to environments artificially generated for experimental purposes. Using fMRI, several brain regions were shown to exhibit an increased HRF during viewing of images depicting spatial environments and natural scenes: the parahippocampal place area (PPA), the retrosplenial cortex (RSC), and the transverse occipital sulcus (TOS) (Aguirre et al., 1996; Epstein and Kanwisher, 1998; O'Craven and Kanwisher, 2000; Maguire 2001; Nakamura et al., 2000; Hasson et al., 2003; MacEvoy & Epstein, 2007). PPA is believed to encode and process the local visual spatial environment, while RSC has been implicated in navigation and

representing the location of scenes in the world (see Epstein, 2008 for a review). TOS has been causally implicated in discriminating spatial environments and natural scene categories using transcranial magnetic stimulation (Dilks et al., 2013). Images showing the location of these regions within the brain can be seen in fig. 1.

Recent work using multi-voxel pattern analysis (MVPA) has investigated the neural mechanisms involved in discriminating natural scene categories (e.g., beaches, forests, city streets, highways, mountains, offices). MVPA classification methods can predict scene category using spatial patterns of neural activation in the primary visual cortex (V1), the lateral occipital complex (LOC), RSC, and PPA (Walther et al., 2009). Additionally, correlating error patterns from each neural classifier with behavioral error patterns generated from a six-alternative forced-choice scene categorization task directly implicated PPA, LOC, and RSC in discriminating natural scene categories (Walther et al., 2009). Further research established that category-specific activation patterns evoked by contour line drawings (which contain structure) are equivalent to activation patterns evoked by color photographs (which contain color, texture, and structure) in PPA and RSC but not in V1 or LOC, suggesting that structural information is of primary importance for the neural processes underlying category discrimination (Walther et al., 2011). While the above studies show that line drawings are perceptually equivalent to color photographs when investigating category identity, no research has investigated the role of structural information in the formation of neural representations for individual scene identity. This study aims to answer the following question: How does the information used to represent scene identity compare to the information used to represent scene category in PPA, RSC, and TOS?

Materials and Methods

Overview. To explore the role of structural information in neural representations for individual natural scenes and identify the features contained within these representations, we employed repetition suppression (RS). RS is an established fMRI effect commonly used in perceptual research to explore the content of neural representations. RS occurs when the same stimulus is presented several times over a short time-period. When a stimulus is repeated, the magnitude of neural activation is significantly less than the magnitude evoked by the initial presentation (Grill-Spector & Malach, 2001). RS can be used to show that two superficially different stimuli are encoded as equivalent in specific brain regions (Turk-Browne et al., 2008). If RS occurs in a brain region for two superficially different stimuli sharing some common feature, then the region in question encodes the two stimuli as equivalent and thus is primarily encoding the common feature.

Recent interpretations of RS hypothesize that the effect relates to the representation of expectation or expectation errors in the brain (Friston, 2005; Summerfield et al., 2008; Turk-Browne et al., 2011). When a subject's expectation for a stimulus is maintained, less neural activation is required to process the stimulus and RS manifests. However, if a subject's expectation for a stimulus is not met, greater neural activation is required to reconcile the expectation error and repetition enhancement (RE) manifests.

In the current study, we used fMRI to measure RS between pairs of color photographs and line drawings in PPA, RSC, and TOS. In two pure conditions, pairs consisted of the same color photograph or the same line drawing. In two mixed conditions, pairs consisted of both a color photograph and a line drawing. By comparing the degree of RS across these conditions, we can infer the features being encoded from natural scenes within a given brain region. If a region

encodes exclusively structural information, then equal RS should be present in all four conditions, because structural information is equally depicted across both presentations in all conditions. If a region encodes information about color, texture, and structure, variable degrees of RS should be present across conditions, depending on the region's function. We hypothesize, based on MVPA studies showing equivalent category-specific activation patterns for line drawings and color photographs (Walther et al, 2011), that PPA, RSC, and TOS will primarily encode structural information from individual natural scenes.

Subjects. Eight subjects (6 male, 8 right-handed, mean age 21.9 years, range 19-26 years) participated in this experiment, which was approved by The Ohio State University Independent Review Board. All subjects had normal or corrected-to-normal vision and provided written informed consent.

Stimuli. Stimuli consisted of color photographs and contour line drawings depicting the same natural scenes from six categories (beaches, forests, city streets, highways, mountains, offices). Color photographs were downloaded off the internet and rated by subjects on Amazon Mechanical Turk as most representative of their respective scene category (Torralbo et al., 2013). Line drawings were created digitally at the Lotus Hill Research Institute by trained artists tracing the contours in color photographs of natural scenes (Walther et al., 2011). Both color photographs and line drawings had a resolution of 800 x 600 pixels. Example stimuli can be seen in fig. 2.

Stimuli were projected on a screen in the rear of the fMRI scanner bore using a Christie DS+6K-M 3-chip SXGA+ DLP projector and subtended 9.52 x 7.14 degrees of visual angle. Stimuli were reflected into the subjects' view using a mirror mounted on the head coil. A fixation point was presented at the center of the screen 500 ms prior to stimulus onset and

remained on screen until 500 ms after stimulus offset. Stimuli were presented for 1000 ms on a neutral gray background. Subjects responded to each stimulus within 1500 ms of stimulus onset using a button pad. Stimulus presentation and response recording were controlled using the open-source VisionEgg software package.

Procedure. Subjects completed 8 main experiment runs lasting 5 minutes and 30 seconds each. Subjects viewed a stream of color photographs and line drawings depicting natural scenes in a fast event-related design. The stream contained embedded pairs of the same image. In two pure conditions, the same color photograph (CP-CP) or line drawing (LD-LD) was presented for both presentations in a pair. In two mixed conditions, either a color photograph (CP-LD) or line drawing (LD-CP) was presented first while an image from the opposing image modality depicting the same scene was presented second. Image presentations within a pair were separated by 3 to 7 items (19.5s-45.5s) to ensure subject ignorance of the second presentation onset. Fig. 3 shows the structure of each condition. Each run was counterbalanced so one pair was presented for each scene category and condition combination, for a total of 24 pairs per run. The inter-stimulus interval (ISI) was randomly jittered between 3 and 6 seconds (ISI distribution mean = 4.5 s) to ensure measurement of the HRF at different points in the curve over the course of the experiment. Subjects completed a natural/manmade category discrimination task for each stimulus presentation. All subjects exhibited near ceiling performance for this task (mean accuracy = 0.97, sem = 0.0065).

Data acquisition. Data was acquired with a 3-T Siemens Trio MRI with TIM and a 12-channel matrix head coil. Functional images for the main experiment were obtained using a gradient echo, echo-planar sequence: TR = 2500 ms, TE = 28 ms, flip angle = 75°, matrix = 74, FOV = 220 mm, 48 transverse 3 mm slices without gap (3 x 3 x 3 mm voxels). Regions of interest were

localized using a separate gradient echo, echo-planar sequence: TR = 3000 ms, TE = 28 ms, flip angle = 75°, matrix = 74, FOV = 220 mm, 48 transverse 3mm slices without gap (3 x 3 x 3 mm voxels). A high-resolution (1 x 1 x 1 mm voxels) MPRAGE T1-weighted anatomical scan (TR = 1900 ms, TE = 4.68 ms, flip angle = 10°) was collected to assist in alignment of echo planar imaging scans.

Data preprocessing. Functional data were motion corrected to a reference volume (50th volume of second main experiment run) to compensate for excessive motion during the experiment. Additionally, functional data were normalized to represent percent signal change and spatially smoothed using a 4 mm full-width-half-maximum Gaussian kernel. The high-resolution anatomical scan was aligned to the same reference volume used in motion correction, and region of interest localizer scans were aligned to the anatomical scan prior to preprocessing. All preprocessing analyses were conducted using the Analysis of Functional NeuroImages (AFNI) toolbox (Cox, 1996).

ROIs. PPA, RSC, and TOS were identified using 2 separate localizer sequences. These sequences contained blocks of color photographs depicting either faces, objects, scrambled objects, or natural scenes. PPA (100 $\pm$ 26 voxels), RSC (106 $\pm$ 63 voxels), and TOS (104 $\pm$ 47 voxels) were defined as clusters of voxels responding preferentially in a linear contrast to natural scenes compared to faces and objects. A maximum threshold of $p < 0.05$ was applied to each contrast, and higher thresholds were applied to break apart clusters. PPA was localized in all 8 subjects, while RSC and TOS were localized in 7 subjects. All voxels contained within each ROI were included in subsequent analyses.

Data analysis. Regressors were created for each condition and trial combination by convolving a fixed HRF with trial onset times. Evoked responses were estimated within subjects using a

general linear model in AFNI (Cox, 1996). Baseline activation magnitudes for each stimulus modality were estimated within-subjects by averaging beta weights from novel color photographs (CP-CP-1 & CP-LD-1) and novel line drawings (LD-LD-1 & LD-CP-1). RS was calculated within subjects in bilateral PPA, RSC, and TOS by subtracting each condition's second presentation beta weight from the same image modality baseline beta weight. For example, RS for the CP-LD condition was calculated by subtracting the CP-LD-2 beta estimation from the line drawing baseline. This method was used to control for potential differences in baseline activation for color photographs and line drawings. For each condition, RS significance was determined across subjects using planned t-tests between baseline beta weights and second presentation beta weights. A Bonferroni correction was used to adjust the t-tests' alpha for multiple comparisons. To compare the degree of RS across conditions, we used a two-way, repeated-measure ANOVA, with first image type (color photograph or line drawing) and pair type (pure or mixed) as factors, paired with a post-hoc Tukey's HSD test. RS analyses were implemented with custom scripts in MATLAB (2011b, The Mathworks, Natick, MA).

Results

In PPA, we observed significant RS for the CP-CP, $t(15) = 5.00$, $p < 0.001$, and LD-LD, $t(15) = 2.81$, $p = 0.013$, conditions. RS for CP-CP remained significant and RS for LD-LD barely missed significance after Bonferroni correction for multiple comparisons ($\alpha = 0.0125$). Significant main effects were found for first image type, $F(1,63) = 5.21$, $p = 0.026$, and pair type, $F(1,63) = 21.17$, $p < 0.001$, and there was a significant interaction between the factors, $F(1,63) = 4.19$, $p = 0.045$. RS was greater for pairs with color photographs first (mean = 0.0983) than for pairs with line drawings first (mean = 0.0406) and greater for pure pairs (mean = 0.128) than for mixed pairs (mean = 0.0113). CP-CP (mean = 0.182) exhibited significantly greater RS than LD-

LD (mean = 0.0729), CP-LD (mean = 0.0143), and LD-CP (mean = 0.0084). RS for LD-LD, CP-LD, and LD-CP was not significantly different. These results are summarized in fig. 4 (a).

In RSC, we observed significant RS for the CP-CP condition, $t(13) = 2.28$, $p = 0.040$, and significant RE for the LD-CP condition, $t(13) = -4.30$, $p < 0.001$. RE for LD-CP retained significance and RS for CP-CP just missed significance after Bonferroni correction for multiple comparisons ($\alpha = 0.0125$). A significant main effect was found for pair type, $F(1,55) = 11.46$, $p = 0.0014$). RS was greater for pure pairs (mean = 0.0779) than for mixed pairs (-0.0472). These results are summarized in fig. 4 (b).

In TOS, we observed significant RS for the CP-CP, $t(13) = 2.74$, $p = 0.017$, and LD-LD, $t(13) = 2.58$, $p = 0.023$, conditions. Additionally, significant RE was found for the LD-CP condition, $t(13) = -2.56$, $p = 0.0237$. RS in CP-CP and LD-LD and RE in LD-CP barely missed significance after Bonferroni correction for multiple comparisons ($\alpha = 0.0125$). Significant main effects were found for first image type, $F(1,55) = 5.08$, $p = 0.029$, and pair type, $F(1,55) = 15.40$, $p < 0.001$, but there was no significant interaction between the factors. RS was greater for pairs with color photographs first (mean = 0.0875) than for pairs with line drawings first (mean = 0.0052) and greater for pure pairs (mean = 0.118) than for mixed pairs (mean = -0.0253). These results are summarized in fig. 4 (c).

Discussion

In PPA, significant RS was found for the CP-CP and LD-LD conditions, with RS in CP-CP being more robust than in LD-LD. The presence of RS for just pure pairs contradicts our hypothesis that PPA primarily encodes structural information from individual scenes. The structure of each scene was equally depicted across all presentations and conditions. If color photographs and line drawings were representationally similar, indicating that PPA primarily

encodes structural information from individual scenes, we would have observed equal RS for mixed and pure conditions. Based on this result, PPA is not just sensitive to an individual scene's structure, but encodes an array of information about a scene's color, texture, and structure. This result is consistent with the theory that PPA encodes the spatial structure of an environment (Epstein, 2008). In order to fully encode a scene and manifest RS, repetition of the exact spatial environment was required. When a scene was repeated with some change in the spatial environment (CP-LD and LD-CP), there was no significant RS. Additionally, greater RS in the CP-CP versus LD-LD condition is expected, given that color photographs have a greater number of repeated features (color, texture, structure) than line drawings (just structure).

In RSC, significant RS was found in the CP-CP condition and significant RE was found in the LD-CP condition. These results indicate that color photographs and line drawings depicting natural scenes have representational differences in RSC, contradicting our hypothesis that RSC encodes primarily structural information from individual scenes. The differential RS and RE across conditions shows RSC is not just sensitive to an individual scene's structure, but encodes information regarding color, texture, and structure. However, unlike PPA, these features must be presented in conjunction (as a color photograph) to elicit a response: no RS was observed when the structural information alone was repeated in the LD-LD condition. The pattern of results supports the theory that RSC encodes and represents aspects of a scene that relate to its naturalness and navigability (Epstein, 2008). In the CP-CP condition a scene is initially encoded as natural and navigable. When the second image is an exact repetition of the first image, this meets a subject's expectation for the naturalness and navigability of the scene, and RS manifests. However, in the LD-CP condition a scene is initially encoded as unnatural and un-navigable. When the same scene is repeated as natural and navigable, this breaks a subjects'

expectation regarding what to expect from the scene, and RE is present to reconcile the expectation error. In the CP-LD condition, there is a non-significant trend towards RE. This trend makes sense given the potential expectation error caused in this condition: a scene initially encoded as natural and navigable is repeated as unnatural and un-navigable. The CP-LD condition may not have displayed the same degree of RE as the LD-CP condition because only one information feature present in the initial presentation of CP-LD was repeated in the second presentation, whereas the only information feature present in the initial presentation was completely repeated in the LD-CP condition.

In TOS, significant RS was found in the CP-CP and LD-LD conditions, mirroring the effects observed in PPA. Additionally, significant RE was found in the LD-CP condition, mirroring the effects observed in RSC. As in PPA, the presence of RS for just pure conditions indicates representational differences between color photographs and line drawings depicting natural scenes in TOS. Based on these results, TOS encodes information about the colors, textures, and structure present in an individual scene, not just the structure as hypothesized. This pattern of results supports the theory that TOS serves as a first pass processing site for natural scenes (Dilks et al., 2013). TOS displays an aggregate of the RS and RE patterns seen in PPA and RSC, indicating that TOS is sensitive to the types of information later represented in both RSC and PPA. TOS may serve as an early extraction site for visual features necessary for higher-level scene processing, extracting these features and feeding them forward to higher-order scene processing areas to facilitate rapid scene processing.

In all brain regions, differential patterns of RS and RE across conditions indicate representational differences between individual line drawings and color photographs. Although previous work has shown the importance of structural information in representing scene category

(Walther et al., 2011), the current study shows that PPA, RSC, and TOS encode information about color, texture, and structure from individual scenes, not just structure as hypothesized. This result highlights an interesting dichotomy in neural scene processing: forming neural representations of scene category requires just structural information, while forming neural representations of scene identity requires information relating to color, texture, structure. Neural representations of scene category contain just features shown to be highly discriminative of scene category (Walther & Shen, under review), while neural representations of scene identity contain a more holistic range of features. Scene sensitive regions may encode a variety of information from natural scenes, then apply specific features to various cognitive processes (e.g., structural information is encoded and used to discriminate scene category). This process would be a highly efficient way to encode and represent the external world, with a holistic range of information being initially encoded to form a natural representation of the scene and subsequent processing activating only representations of features most applicable to a specific cognitive process.

This interpretation is complicated by two methodological differences between earlier studies investigating category identity and the current study: event-related versus blocked designs and RS versus MVPA. In event-related designs, each trial consists of a single image. In blocked designs, each trial consists of multiple images sharing some feature (e.g., scene category) presented immediately back-to-back. Additionally, recent research has highlighted that RA and MVPA often provide inconsistent results, possibly because each effect captures different aspects of neural processing (Epstein & Morgan, 2012). One hypothesis is that MVPA reveals clustering of features represented by local neuronal populations, while RS reveals more widespread neural processing relating to top-down processes such as expectation (Epstein &

Morgan, 2012). Whereas the current study uses an event-related design and RS, earlier studies investigating the representation of category identity (Walther et al., 2009; 2011) used blocked designs and MVPA. Additional MVPA analyses on the current dataset would help clarify these potential methodological confounds. Using MVPA classification to predict scene category from event-related data and investigating whether the equivalence of activation patterns for color photographs and line drawings holds would determine whether the sufficiency of structural information to represent category identity is true for individual scenes and would provide further evidence applicable to the ongoing debate regarding the actual neural processes measured by MVPA and RS.

Finally, the current study offers several possible avenues of follow-up research. Further research could focus on identifying what cognitive processes (e.g., memory, attentional allocation, contextual cueing) are supported by neural representations of the colors and textures present in natural scenes and further investigate whether these processes are supported by structural information. Additionally, future research may focus on identifying how color, texture, and structure are differentially encoded and represented across PPA, RSC, and TOS.

Conclusion

We have shown that color photographs and line drawings depicting natural scenes are representationally dissimilar in PPA, RSC, and TOS, indicating that these regions encode an array of information from individual natural scenes, including color, texture, and structure. This result highlights a dichotomy regarding what information is contained in neural representations for scene category identity compared to individual scene identity. Representations of scene category contain primarily structural features, while representations of scene identity contain a more holistic range of features. Observed patterns of RS and RE support existing theories that

PPA encodes spatial layout, RSC encodes aspects of a scene's naturalness and navigability, and TOS serves as a first pass processing site for natural scenes.

Figure 1

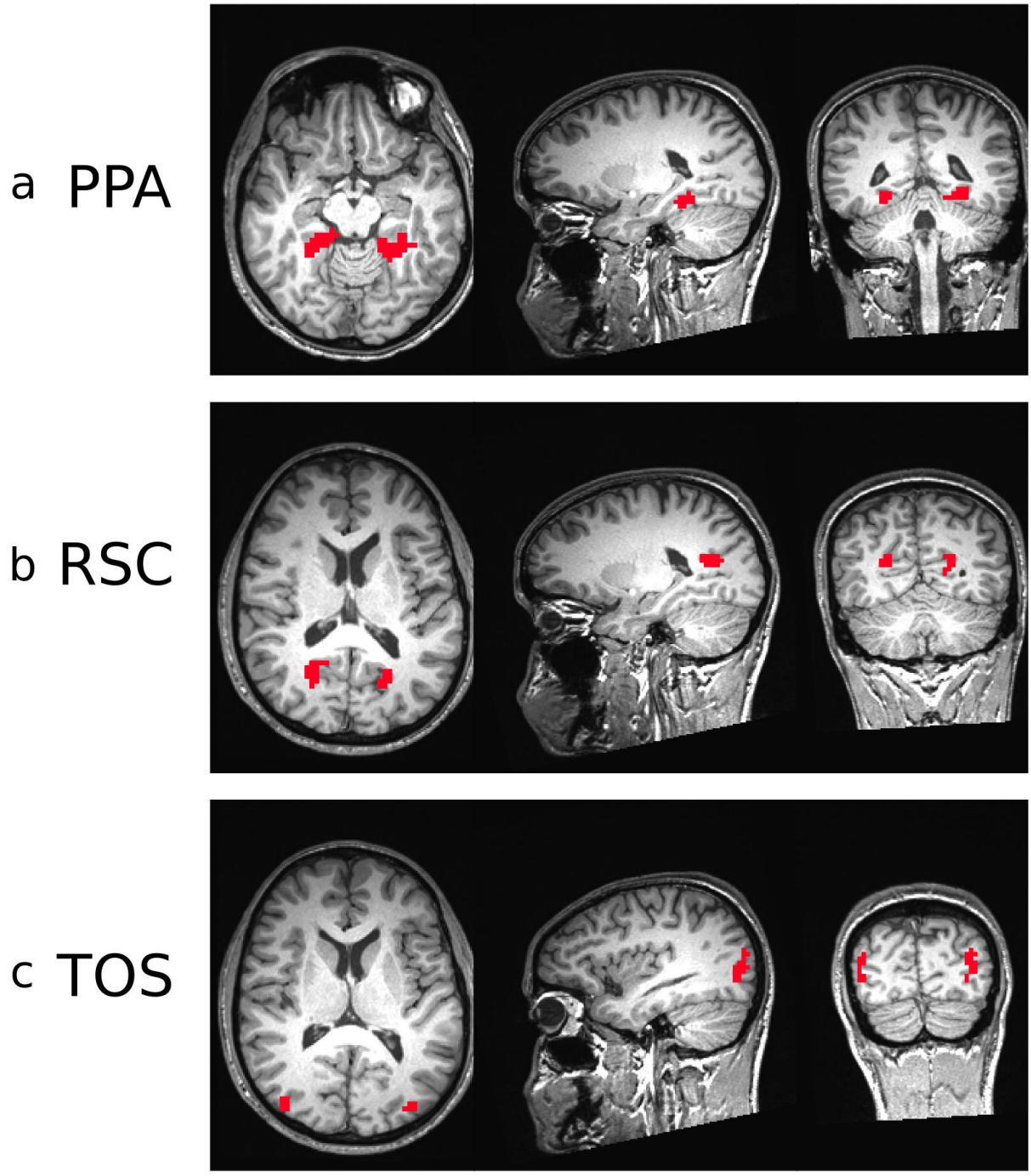

Fig. 1. Location of the parahippocampal place area (PPA) (a), retrosplenial cortex (RSC) (b), and transverse occipital sulcus (TOS) (c) in one subject.

Figure 2

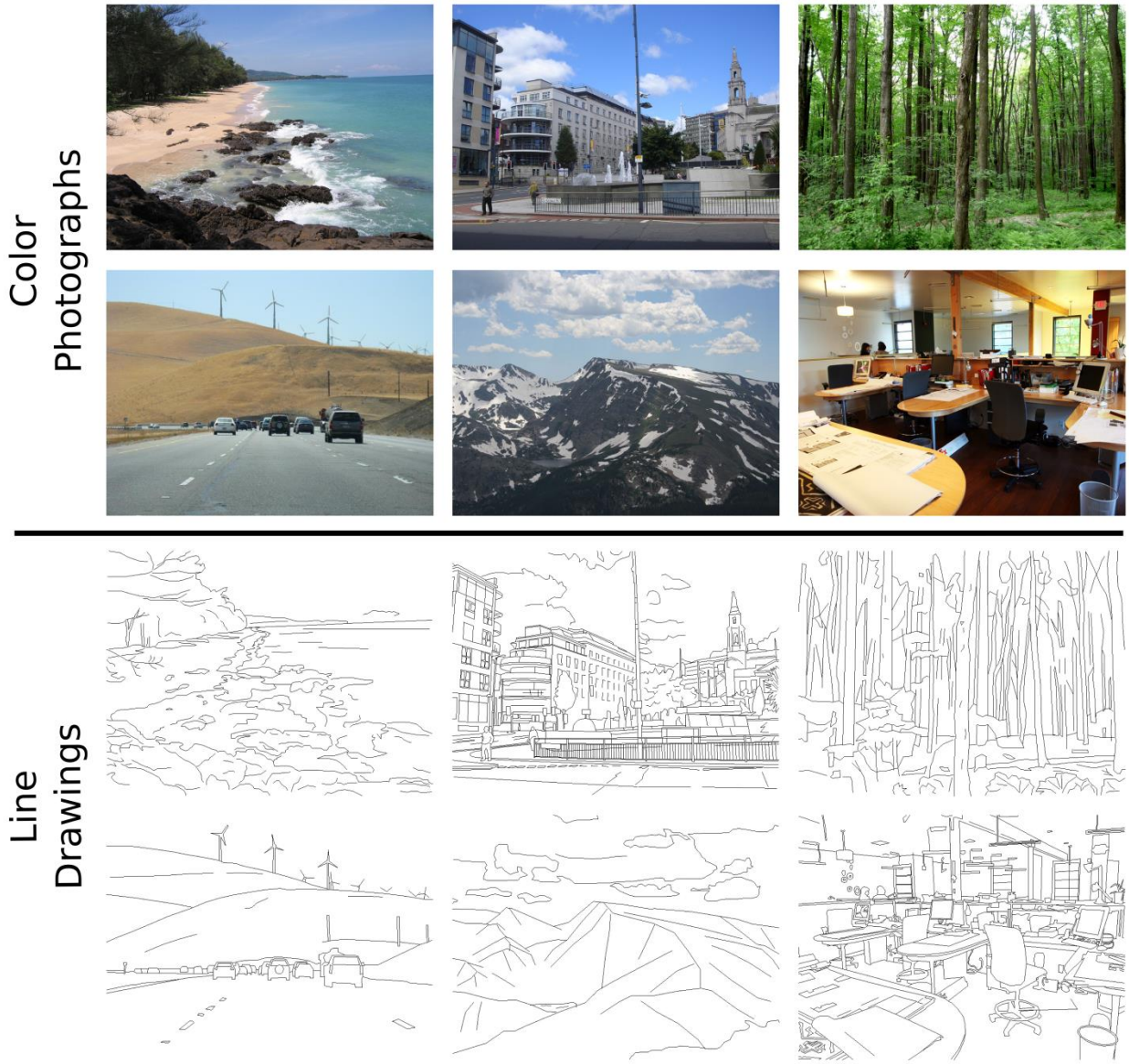

Fig. 2. Sample images from the experiment. Images depicted scenes from six different categories: beaches, city streets, forests, highways, mountains, offices.

Figure 3

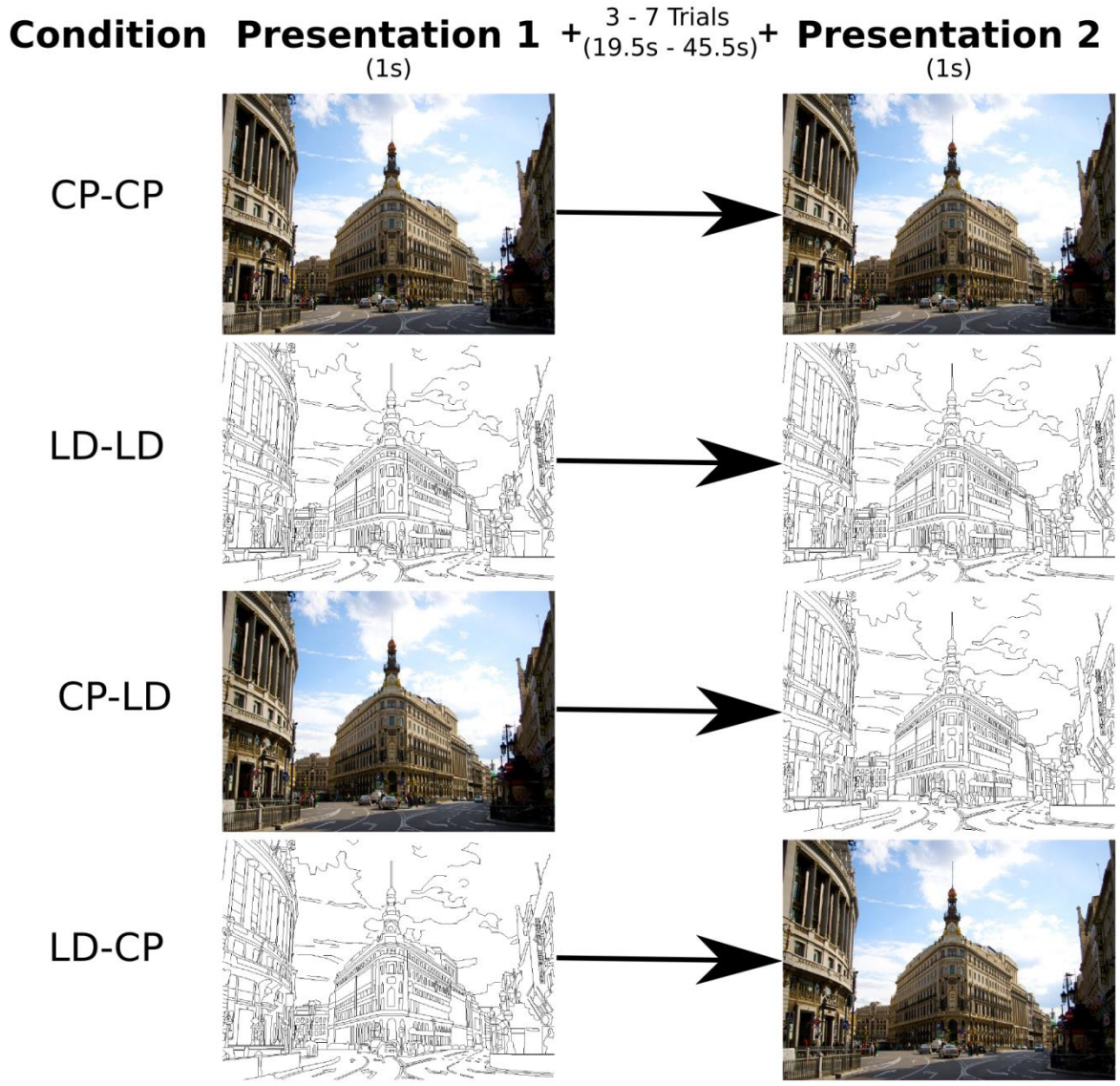

Fig. 3. Condition structure for experiment. Images were presented for 1s in a constant stream and images within a pair were presented 3-7 trial apart.

Figure 4

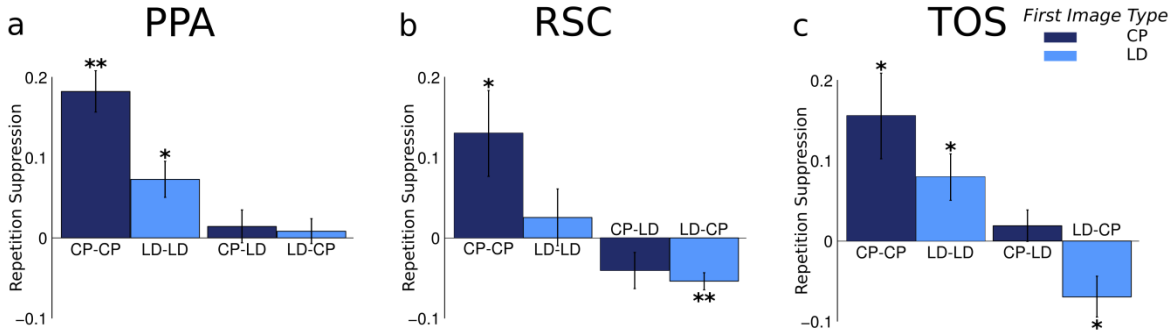

Fig. 4 Repetition suppression results for PPA (a), RSC (b), and TOS (c). Repetition suppression significance (t-test) is indicated. Error bars represent standard error of the mean. For full ANOVA results, see Results section. * $P < 0.05$. ** $P < 0.01$.

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